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Vol. 45 No. 8

BULLETIN

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TORREY BOTANICAL CLUB

AUGUST, 1918

The evolution of maize

PAUL WEATHERWAX

(WITH THIRTY-SIX TEXT FIGURES)

The ancestry of Indian corn, the place of its origin, and its relation to other plants of its family have been the subjects of extensive study and discussion. As a New World contribution to science and agriculture, the maize plant found, after a time, its present systematic position, and it has made its way into a place of prime importance in the economic life of the world.

When first seen by the civilized explorers of this country, maize was a cultivated plant; and no wild form of it has ever been found. Theories maintaining that it was of Old World origin have been shown to lack sufficient proof, and it is now very generally believed to have originated somewhere in the plateau region of Mexico or Central America.

Concerning the ancestry of maize a number of different theories have been advanced. In 1892 Bailey (1) expressed the opinion that *Zea canina*, which had been described a short time previously, was the progenitor of maize. Harshberger's work (17), published in 1893, was also based upon the assumption that this was the primitive maize plant. The latter authority and others have since shown that *Zea canina* is a hybrid between teosinte and ordinary maize. In 1911 Harshberger (20, pp. 51–52) described, as the theoretical ancestor, a plant whose inflorescence would resemble that of *Tripsacum;* and in 1912 he suggested (21, p. 399) that

[The Bulletin for July (45: 259–308. *pl. 8*) was issued August 9, 1918.]

"our maize is of hybrid origin, probably starting as a sport of teosinte, which then crossed itself with the normal ancestor, producing our cultivated corn." Characterizing these earlier theories is Häckel's suggestion, made (**16**, p. 20) as early as 1889, that the female spike of corn was evolved by monstrous fasciation, from a number of parts like the lateral branches of the male inflorescence. In 1906 Montgomery (**24**) described a theoretical ancestor of maize and pointed out the fact that the ear is not the fasciated homologue of the lateral branches but the equivalent of the central spike of the tassel. Mrs. Kellerman had given a similar interpretation of the case in 1895, but her article (**22**) seems not to have been available to many botanists. In 1912 Collins made the point (**9**, p. 525) that the homology between the ear and the central spike of the tassel is inconclusive, because the central spike of the tassel is as anomalous and as hard to explain as is the ear. He discussed two theories as to the structure and origin of these organs and favored the idea that they are the results of fasciation. According to his theory, ordinary maize originated as a hybrid between teosinte and some plant possessing the characters of pod corn. In 1912 East (**12**) discussed the origin of maize and said that he agreed, in a way, with both Collins and Montgomery.

These are the more comprehensive discussions of the subject, but the discovery of an abnormal ear or tassel, a new variety, or an unusual habitat for the plant has, from time to time, been enough to provoke a new theory or a modification of an old one.

The present status of the question may be summarized as follows: most of the evidence concerning the evolution of maize has come from a comparison of its gross morphology with that of its near relatives, and from a study of hybrids between maize and teosinte; the ear of corn is generally supposed to be a fasciated structure; two theories are now held as to the origin of the plant—(1) that maize and teosinte have descended along slightly different lines from a common ancestor, and (2) that maize originated in a cross between teosinte and some closely related grass.

But in a detailed examination of maize and its near relatives, we meet with many inconspicuous but significant organs which have not thus far been considered in any theory of the evolution

of the plant. The writer has made a thorough study of many varieties of corn, probably representing the full range of variability of the species, and other species of the Maydeae have been examined in detail by way of comparison. As a result of these studies, a theory is here proposed, which is believed to explain, in a manner more consistent with known facts, the evolution of maize.

Acknowledgment is here made of valuable assistance received in this study from a number of sources. The investigation is an outgrowth of a problem suggested to me five years ago by Professor D. M. Mottier, who has since then also aided me with many suggestions and criticisms. American consuls in several cities of Central and South America have assisted me in getting seeds of many varieties of corn; and very material assistance of the same kind has been given me by a large number of friends in this country. The Bureau of Plant Industry has supplied me with seeds of corn and teosinte. Rhizomes of *Tripsacum* were obtained from the Missouri Botanical Garden. The late Mr. Juan J. Rodriguez, of Guatemala, sent me rhizomes of a species of *Tripsacum* and seeds of a number of varieties of corn; he also told me of many interesting observations that he had made on the grasses of Guatemala. Mr. George F. Will, of Bismarck, North Dakota, supplied me with seeds of thirty varieties of corn collected from Indian reservations. Mr. A. Heinisch, of Clarcona, Florida, sent me seeds and morphological material of teosinte, aided me in making observations in his teosinte fields in the summer of 1917, and gave me the benefit of many observations that he had made as a grower of the plant.

CLASSIFICATION

The tribe Maydeae includes a number of grasses characterized by unisexual spikelets, the male being above the female, in the same or in different inflorescences. The seven genera of the tribe fall naturally into two classes. *Zea*, *Euchlaena*, and *Tripsacum* bear evidences of close relationship and are all native of America. Having the same general characteristics as these, but differing from them somewhat in appearance and detailed structure, are four genera, *Coix*, *Chionachne*, *Sclerachne*, and *Polytoca*, which

are all native of southeastern Asia and the neighboring islands. An anomalous American genus, *Pariana*, has been included in this tribe by some authorities, but its natural position seems to be in another group.

The best evidences concerning the immediate ancestry of maize come from a comparative study of the three American genera of the Maydeae. The Asiatic species are probably much less closely related to those of America than they are to each other; and, for present purposes, they will not be considered in detail.

FIG. 1. A variety of corn from an Indian reservation; this plant may be considered the type of the species, which is today essentially the same as when first seen by the white man.

Zea and *Euchlaena* are sufficiently closely related to cross readily, and there is a record of at least one case of hybridization of *Euchlaena* and *Tripsacum;* but I have found no record of any hybrid between *Zea* and *Tripsacum*.

MORPHOLOGY OF ZEA

The genus *Zea*, represented by the single species, *Zea Mays* L., comprises all the varieties of maize. Being the best known species of the Maydeae, it is taken as the basis for comparison. It is a very variable species, but its variability is mostly quantitative in character. Good general descriptions of the plant have been available for a long time, but some significant details have not thus far been included in any of these. A complete working description makes necessary here the repetition of some well-known facts as a proper background for new details.

The aerial part of the typical maize plant (FIG. 1) consists of a tall, jointed stem, provided with distichous leaves, and bearing in the axil of each leaf, except possibly some of the upper ones, a potential branch. Some of these branches do not normally develop, and microtome sections are sometimes necessary to disclose their rudiments. One or more near the middle of the stem develop into ear-bearing shoots. The lowest branches, arising at or below the surface of the ground, become the well-known "suckers" or "tillers." The main stem terminates in a male inflorescence.

FIG. 2. A typical male inflorescence of corn.

FIG. 3. Portion of the central spike of a corn tassel. FIG. 4. A group of spikelets, such as often occurs instead of a pair. FIG. 5. Spikelets on the lateral rachis of a corn tassel.

Male inflorescence.—The terminal panicle of spikelets (FIG. 2) is made up of a number of simple or branched lateral organs attached to a central axis which terminates in a spike. The spikelets are borne in pairs, one pedicelled and the other sessile (FIGS. 3, 5). Occasionally in all, and very regularly in a few varieties, groups of three or more are found (FIG. 4), instead of pairs of spikelets, and in such a group one is usually pedicelled. Both of a pair or all of a larger group are occasionally sessile. In the typical

case, where the spikelets are paired, the pedicelled ones are arranged symmetrically in a horizontal plane along the sides of the lateral rachis, and the sessile ones are ventral to these on the rachis, giving the structure a definite dorsoventral aspect (FIG. 5). The central spike is symmetrical with respect to the pairs of spikelets, which are arranged in several longitudinal rows upon it (FIG. 3).

The spikelets have been described in detail elsewhere (**25**, **26**). Each has two flowers and a full complement of glumes, palets, and lodicules. Only the male essentials are functional, but each flower has a rudimentary pistil. A superabundance of pollen is produced, and it depends upon gravity and the wind for distribution. The flowering period of an individual plant is limited to two or three weeks, depending upon weather conditions and the size of the inflorescence.

FIG. 6. An ear of corn whose husks have laminae.

Female inflorescence.—The ear-bearing branch has the same general structure as the main stalk, except that its inflorescence is female; and the shortness of its axis enables the leaf sheaths to cover the inflorescence and mature fruit. In some cases the laminae and ligules of these prophylla are present (FIG. 6), but often they are lacking (FIG. 7). In the axil of each prophyllum is a bud which may develop into an ear-bearing shoot (FIG. 8). This behavior is common to some varieties, and it seems possible to bring it about in any variety by subjecting the plant to proper physiological conditions. The clusters of ears formed in this way and occurring in ordinary maize (**6**, *f. 96, 97*) or in teosinte-maize hybrids (**17**, *pl. 1*) are not at all to be confused with branched ears of maize (FIG. 9). They have much the same appearance to the casual observer, but they have a different origin and a different

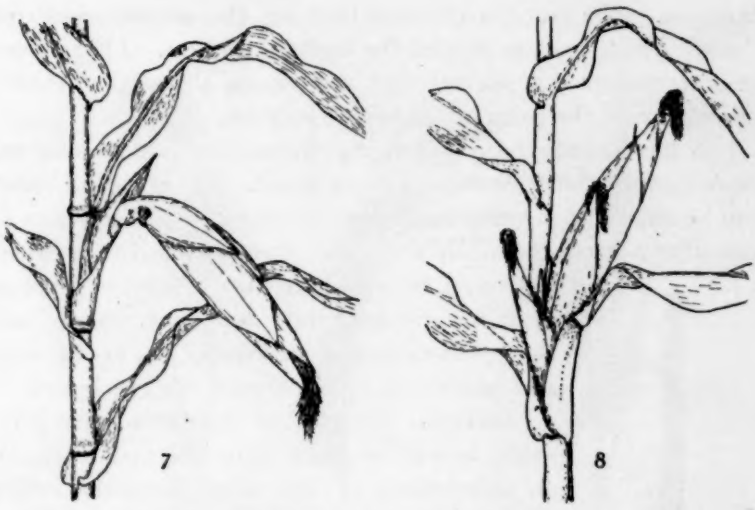


FIG. 7. An ear-bearing shoot of a high-grade dent corn. The prophylla have lost their laminae and ligules. FIG. 8. An ear branch bearing small lateral ears.

meaning. When these secondary branches develop far enough, buds are formed in the axils of their prophylla, indicating the possibility of tertiary branches.

The female spikelets are borne in pairs, sessile or almost so, on a thickened axis, the whole structure being the "ear." The "cob" is the axis of the mature ear after the grains have been removed. Each row of pairs of spikelets is responsible for two rows of grains on the ear, thus accounting for the fact that an ear always has an *even* number of rows. The spikelets are two-flowered and have the same parts as those of the male inflorescence; but the whole lower flower of each is aborted, the lodicules are present only in early stages of development, and the stamens are aborted. The pistil of the upper flower is usually the only functional organ of either flower, but occasionally in any plant, and as a fixed characteristic of some varieties, the pistil of the lower flower may also

FIG. 9. Ateratological ear suggesting the relationships between the normal ear and the central spike of the tassel.

function. The pistil is characterized by the greatly elongated "silk," which reaches beyond the husks of the ear. I have given in other papers (**25**, pp. 131–137, and **26**, pp. 488–493) a detailed description of the parts of the female spikelet.

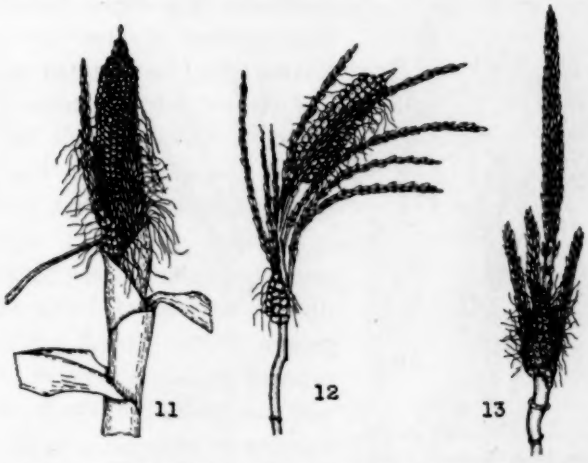
As has already been noted, the normal ear is doubtless the homologue of the central spike of the tassel. Every part of either can be identified in the other, and they bear identical relations to the other parts of the shoots which they terminate. The apparent difference between the two is one of development. Teratological forms (FIGS. 9, 10) and the inflorescences of suckers (FIGS. 11–13) suggest connecting links between the two organs.

FIG. 10. A teratological ear having the upper part metamorphosed into a male spike.

Suckers.—The sucker branches may arise singly or two or more from one node (FIG. 1), an appearance of the latter condition often being the result of secondary branching. Most of the suckers develop root systems more or less independent of that of the main plant. Some suckers have all the appearance of ears growing low on the stalk; others grow tall and become structurally and functionally the same as the main stalks; and still others have characteristics intermediate between these two extremes. These intermediate types, while they have axillary buds, usually develop only terminal inflorescences, which may represent any possible gradation between an ear and a normal tassel (FIGS. 11–13). The most ear-like of these have, no doubt, been made the subject of many of our popular articles on freak ears. The figure given by Mrs. Kellerman (**22**) and some of Montgomery's photographs (**24**) look suspiciously like sucker inflorescences. Many freak ears given to me by non-technical collectors have turned out, on close inquiry, to have been taken from suckers. Their value as evidences of evolution are none the less for this; but they must be interpreted in a different way, for they are not in any way teratological.

Variations.—Anomalous inflorescences are common, however,

and there are several more or less definite varieties of maize



FIGS. 11–13. Normal terminal inflorescences of suckers, having characteristics of both the ear and the tassel.

which do not agree with the general description just given. A well-known variation is found in pod corn, each mature grain of which is covered by the enlarged glumes of the female spikelet. Many plants of pod corn have perfect or female flowers in their tassels and produce fruits there, and some of these plants have a tendency to become earless; but no independent earless variety has ever been isolated. Other varieties of maize occasionally produce female flowers in the tassel, probably as a result of physiological conditions. It is significant that silks produced in the tassel are usually fasciated like those of the normal female flower, but bipartite silks have been seen in a few cases. Most female spikes of maize have sterile tips, and these are often re-

FIG. 14. A tassel of Gernert's Branch Corn.

placed by staminate spikes (FIG. 10). Emerson (13, p. 83) has isolated a dwarf variety which has perfect flowers in the ear. Gernert (15) has isolated from a yellow dent variety a strain in which the ear is a loose panicle like that of one of the sorghums. The tassel is also branched more than in the typical variety (FIG. 14), and many groups of spikelets are borne on peduncles instead of being in sessile groups (FIGS. 15–19). A common type of variation consists of a normal ear bearing a whorl of small, four-rowed branches around the base (FIG. 9). Ears variously divided or branched at the tip are also of common occurrence.

FIGS. 15–19. Peduncled groups of spikelets from Branch Corn, showing the probable steps in the evolution of the pair of spikelets.

MORPHOLOGY OF EUCHLAENA

Without discussing the systematic treatment of *Euchlaena*, we may take *Euchlaena mexicana* Schrad. (synonymous with *Euchlaena luxurians* Dur. and *Reana luxurians* Dur.) as the type of the genus. It is the well-known teosinte, an annual forage plant of the warmer parts of America. The species is much less variable than maize.

Teosinte has much the same general appearance as maize, especially since the casual observer's mental picture of the latter is obtained from seeing two or three plants growing in a clump. It has the same sort of leafy stem, and the same potential branches in the axils of its leaves; but the branches arising from the base of the plant—ten to sixty or more in number—grow as tall as the main stem and resemble it in every way. These continue to branch indefinitely, a branch being possible at practically every node; generally speaking, a branch has about as many nodes as the main stalk above the point of branching. The main stalks and some of the higher branches are terminated by male panicles. At the top of any stem, the branches tend to be male, while the lower ones of the same order tend to be female.

The plant makes a very ready response to conditions of soil and climate, and herein lies the main cause of its variability.

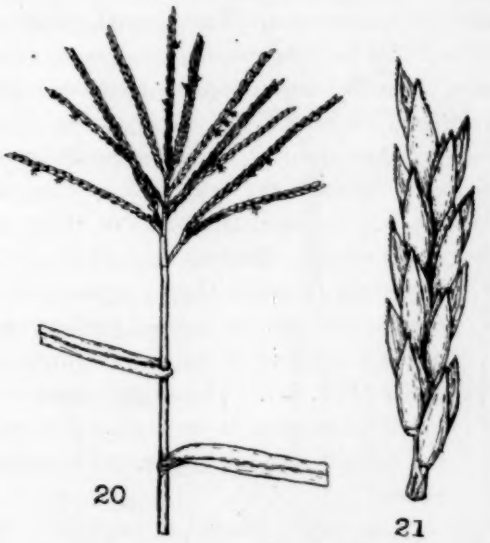


FIG. 20. Tassel of teosinte FIG. 21. Portion of a spike of a teosinte tassel.

Rich, wet soil and warm weather are most favorable for luxuriant growth. Plants are not injured by standing for some time in water a foot deep. Under favorable conditions the stems often

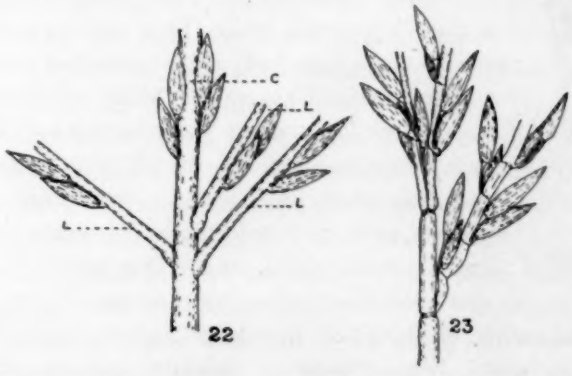


FIG. 22. Portion of a corn tassel. The lateral spikes, *LL*, are jointed to the main axis, which continues into the central spike, *C*. FIG. 23. Part of a tassel of teosinte; all the spikes are jointed to the main axis.

fall prostrate, take root at the nodes, and send up branches, becoming almost if not quite perennial at times.

Male inflorescence.—The male panicle (FIG. 20) resembles that of maize in appearance. The lateral spikes are so much alike in the two that a close examination is necessary to reveal any difference; but the central spike, which is characteristic of maize, is lacking in teosinte. All the branches (FIG. 21) of the teosinte tassel are dorsoventral, and it is probable that they are all morphologically lateral, the true end of the axis being not in any one rachis but between the bases of the uppermost two. This is further supported by the fact that all the tassel branches, including that (or those) apparently occupying a central position, are jointed at their bases (FIG. 23), which is not true of the central spike of the tassel of maize (FIG. 22). This organ seems merely to have failed to develop in teosinte. Following anthesis, the rachids become brittle, easily separating at the nodes.

FIG. 24. A female spike of teosinte.

The male spikelet is much like that of maize. The same parts are present, including the rudimentary pistils, and, in so far as has been observed, there is no significant difference in the development or the final form of the two. The pollen and pollination are as in maize.

Female inflorescence.—The female inflorescence is usually a single spike (FIG. 24), enclosed in the sheath of a single leaf, which often has a ligule and a short lamina (FIG. 25). Many of these shoots, each borne on a short stem in the axil of a leaf, may be enclosed in the sheath of a larger leaf of the main stem, and the silks, protruding from the sheath, give the whole the appearance of a young ear of maize (FIG. 26). This whole structure is the equivalent of an ear-bearing shoot of maize, having branches of the third, fourth, or higher orders, but with the characteristic female spike of teosinte, instead of an ear, borne on each branch.

The female spike has received the most unsatisfactory treat-

ment of any part of the plant. As a typical instance of misinterpretation of its structure may be cited a statement in a recent textbook (2, p. 137), where it is spoken of as being made up of kernels fastened end to end, the whole structure having nothing to correspond to the cob in maize. Collins's description (9, p. 525) of the spike as "one-rowed" is equally misleading.

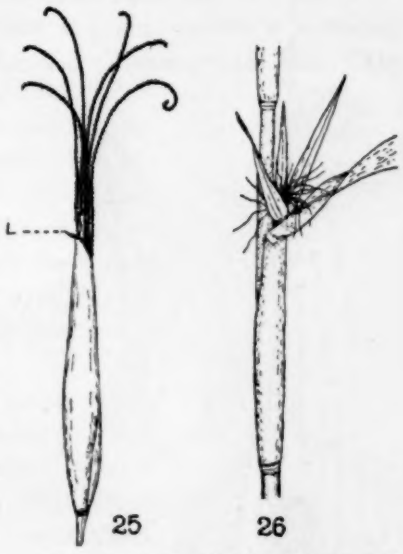


FIG. 25. An "ear" of teosinte, covered by its single husk, which has a rudimentary lamina, *L*. FIG. 26. Portion of a stem of teosinte bearing a cluster of female spikes.

This spike is made up of two rows of functional spikelets borne alternately in alveoli in the rachis; by the side of each of these spikelets there is a small rudimentary structure (FIGS. 27, 28) which represents the other spikelet of the pair. Structurally, then, the spike has four rows of spikelets. It will be remembered that in the male spike the pedicelled spikelets are symmetrically arranged on the rachis, with the sessile ones below them; but, in the female spike, the fully developed sessile spikelets occupy the symmetrical positions, and the rudimentary pedicelled ones have been crowded up to a dorsal position (FIGS. 34, 35). In teosinte somewhat mixed with maize the rudimentary spikelet is sometimes replaced with a sterile or male, pedicelled one, and a little further contamination with maize produces two functional female spikelets side by side. Paired female spikelets are also occasionally found in pure teosinte. These facts indicate that the female spike is the homologue of one of the branches of the tassel, and it probably does not morphologically terminate the shoot of which it is a part.

The female spikelet consists of the same parts as that in maize. The lower flower is aborted, rudimentary stamens are present,

and the development of no part shows any significant difference except for the indurated outer glume. The silk has much the same structure as in maize, but it is shorter.

Because of the large number of inflorescences, the flowering period of a teosinte plant is much longer than that of a maize plant, and the chances for self-pollination are better. When the

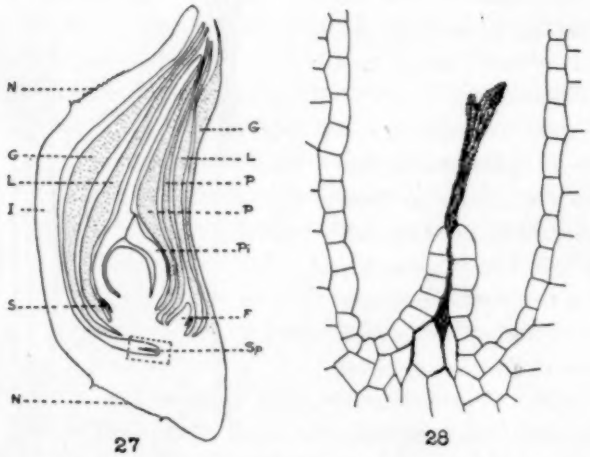


FIG. 27. Diagram of a longitudinal section of an internode and its spikelet in the female spike of *Euchlaena* or *Tripsacum*. *NN*, nodes; *I*, internode; *GG*, glumes; *LL*, lemmae; *PP*, paleae; *S*, rudimentary stamen; *F*, rudimentary flower; *Pi*, functional pistil; *Sp*, position of the rudimentary spikelet, which does not appear in a median section. FIG. 28. The rudimentary spikelet shown in the dotted rectangle in FIG. 27.

seeds are mature, the female spike separates at the nodes, each internode bearing a spikelet and its enclosed fruit.

Mixed inflorescences.—The homologies suggested between the male and female inflorescences are further indicated by the occurrence of mixed inflorescences. In male tassels, functional female spikelets have several times been observed near the base of one or more of the branches; and the sterile tip of the female spike, as in maize, is often replaced by a short staminate portion (FIG. 29). Some single spikes are so much like those of *Tripsacum*, to be described later, that it would be hard to determine whether it is a case of male spikelets being in a female inflorescence, or vice versa. In such a mixed spike, each male spikelet is usually

accompanied by another male or sterile one; and each female spikelet is characteristically alone, has an indurated outer glume, and is sunken into the rachis. No functionally bisexual spikelets have been seen, but it must be emphasized that all are structurally so.

FIG. 29. A mixed spike of teosinte.

MORPHOLOGY OF TRIPSACUM

A number of species of *Tripsacum* are native of various parts of America, but the best known is *Tripsacum dactyloides* L., the gama grass of swamps and stream banks of the central and southern parts of the United States. Being the only species available for my work, it is the basis of my conclusions for the genus.

Tripsacum dactyloides (FIG. 30) is perennial by means of a branched rhizome, from the nodes of which arise the aerial shoots. Many of these are sterile, and their stems are so short that only the leaves appear above the ground. In early summer, however, some of the shoots elongate for flower bearing and show the adult structure. These stems attain the height of four to six feet and resemble somewhat those of maize or teosinte. The flowering period continues for two or three months. The main stem bears a branch at each node, and this has secondary and even tertiary branches. The main stem is terminated by a panicle, and each branch by a spike or a panicle. Erect or curving until after flowering, the stems are, by means of some growth-mechanism near the base, caused to lie prostrate by the time the seeds are mature.

Inflorescence.—The male spikelets occupy the terminal and the female the basal part of the same spike (FIG. 31). The mode of branching of the panicle is similar to that in the male inflorescence of *Euchlaena*. There is no evidence of any central spike, all the branches being much alike.

There is a very evident tendency for the highest inflorescence,

that is, the one terminating the main stem, to be male, and the lower ones, terminating the branches, to be female. Counts of male and female spikelets in a number of inflorescences showed in those of the main stem a ratio of 1 female to 18.5 male; in those of the primary branches the ratio was 1 to 7.5; and on secondary branches the ratio was still higher. No unisexual inflorescence has been observed, however, on any plant.

FIG. 30. Habit of *Tripsacum dactyloides*.

Male spikelets.—The male spikelets are arranged on the rachis in two rows of pairs; and the male portion of the spike, even where there is but one spike in the inflorescence, has the same dorsoventral appearance as in maize or teosinte (FIG. 32); one spikelet of a pair sometimes has a short pedicel, but both are usually sessile. The rachis of the male part of the spike becomes brittle soon after the pollen is shed.

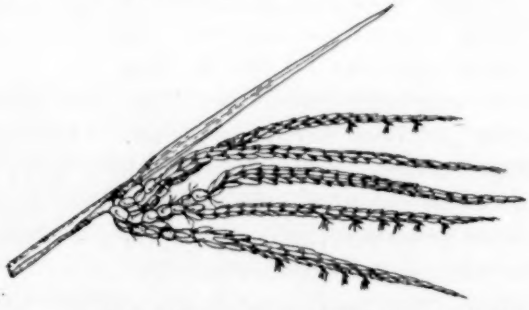


FIG. 31. Terminal inflorescence of *Tripsacum dactyloides*.

The outer glume of the male spikelet is somewhat thickened and hardened, but otherwise the bracts, lodicules, stamens, and rudimentary pistils are essentially the same as those of maize or teosinte.

Female spikelets.—The female portion of the spike (FIG. 32) is similar to that of teosinte, but there is usually more or less external evidence of dorsoventrality. The spikelets are alternately imbedded in alveoli in the rachis, forming two rows arranged almost symmetrically or along one side of the rachis. But the real four-rowed structure is clearly indicated, as in teosinte, by the presence of a rudimentary spikelet (FIGS. 27, 28) near the base of each functional one. This rudiment is sometimes replaced by a functional spikelet, which may be either male or female (FIG. 33). As in teosinte, the female portion of the spike easily separates at the nodes when the seeds are mature.

FIG. 32. Portion of a spike of *Tripsacum*, showing paired male and solitary female spikelets. FIG. 33. Pair of female spikelets sometimes found in *Tripsacum*.

The female spikelet has the same parts as that of teosinte, and they are arranged in the same way. The stigma is bipartite (FIGS. 32, 33), in contrast with that of *Zea* or *Euchlaena*.

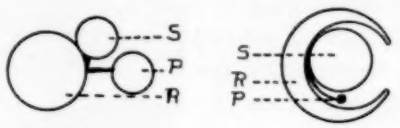
Seeds.—The plants that I have grown ordinarily set seeds in only a few flowers, and these do not germinate well. Mr. Rodriguez has informed me that *Tripsacum laxum*, a Central American species, has never been known to produce seeds. The morphological basis of this peculiarity has not been determined, but it is doubtless correlated with the perennial habit.

SUMMARY OF MORPHOLOGY

As is evident from the foregoing descriptions, these genera are identical in structural plan; for every significant organ in any one of them, there is a homologue, fully developed, rudimentary, or indicated, in each of the others.

Common to all three is the jointed vegetative stem, bearing a leaf or a leaf rudiment at each node and a branch or a bud in the axil of almost every leaf. Buds, representing undeveloped shoots, bear no indication of giving rise to branches, because their nodes have ordinarily not developed far enough; but practically every fully developed node has a bud.

Some of the stems of *Tripsacum* live underground, thus making the plant perennial, a condition which, in some of the species at least, is associated with the swamp habitat and limited seed production. When *Euchlaena* grows in a swampy place, it has a tendency to assume the perennial habit by means of prostrate



34 35

FIG. 34. Diagram of a cross section of one internode of a male spike of maize or teosinte, showing the rachis, *R*, with one sessile, *S*, and one pedicelled, *P*, spikelet. FIG. 35. Section of an internode of a female spike of *Tripsacum* or *Euchlaena*, showing a functional sessile, *S*, and a rudimentary pedicelled, *P*, spikelet imbedded in the rachis, *R*.

stems rooting at the nodes; its seed production, however, seems in no way impaired by this habit. Maize produces a large number of viable seeds and has no tendency to become perennial.

The general inflorescence of the group is a panicle with a central spike and lateral branches, like the tassel in maize. In most of the inflorescences some parts of this general structure are lacking; in the maize ear it is the lateral branches, and in the teosinte tassel and the inflorescence of *Tripsacum* it is the central spike; in the female spike of *Euchlaena* all that is present is a single lateral branch. The spikelets occur usually in pairs, but sometimes in larger groups, in all the inflorescences.

The spikelet has two glumes and two florets. Structurally the flowers are as in the typical grass, but the regular suppression of some of the essentials makes all the flowers functionally unisexual. *Tripsacum* has two feathery stigmas, but the homologue of these in *Zea* and *Euchlaena* is the silk, a fasciated organ divided at the tip.

THEORIES OF THE EVOLUTION OF MAIZE

As has been noted by way of introduction, several theories have been advanced to explain the origin of the maize plant or some of its parts; and it is appropriate here to examine in a critical way some of the more prominent of these.

Origin of the ear.—Most of the attempts to explain the structure and origin of the ear of corn have been based upon Hackel's idea (**16**, p. 20) that it has resulted from the union of several organs like the lateral branches of the tassel. Harshberger at first supported this theory (**17**, pp. 75–83); after describing the ear and some of its teratological variations, he says: "These structural and teratological arrangements point to the probable union of several spikes into a thick, fleshy axis, with grains on the circumference, each paired row limited at the sides by a long, shallow furrow, a row corresponding to a single spike of *Euchlaena* or *Tripsacum*." Gernert (**14**, p. 37) agrees with Harshberger in support of the fasciation theory and gives some additional evidences, most of which, however, are irrelevant or obviously open to objection. Mrs. Kellerman (**22**) and Montgomery (**24**) object to this theory and point out that the ear is the homologue of the central spike of the tassel; and later (**20**, p. 51) Harshberger apparently agrees with the former. Collins (**9**, p. 525) removes all doubt of this homology and shows that the central spike of the tassel is as anomalous and as much in need of explanation as is the ear. He thinks it probable that both have resulted from fasciation. One of the latest discussions of the structure of the ear is that given by Worsdell (**28**, p. 58). Due to a special definition of terms, he does not call this a case of fasciation; but, as the following statement indicates, he is in accord with most of the others in his interpretation of the structure and origin of the ear: "It consists of the fusion of numerous spikes with flattened rachis, each bearing two rows of female spikelets, to form the thick female inflorescence usually termed the 'cob.'" (The word "cob" is a misnomer; he is evidently talking about an ear.) A new term, "disruption," is proposed to cover the *abnormality*, which "consists in the appearance of a 'cob' as a copiously-branched paniculate inflorescence, closely resembling, in its extreme form, the male inflorescence; and is due to the dissolution of the compound organ into its separate parts."

In spite of the apparent consistency of this widely accepted theory of the formation of the ear, it is untenable at least in its present form. There can be no reasonable doubt of the homology between the ear and the central spike of the tassel. Ears termin-

ated by male spikes (FIG. 10), ears with small female or mixed branches attached (FIG. 9), and perfect ears replacing the central spikes of sucker tassels (FIG. 12) all give indication of this. Moreover, the early development of the two organs is the same except that in the case of the normal ear no side branches are developed. But the idea that either or both of these organs is fasciated is inconsistent with some important morphological facts. Carefully prepared microtome sections fail to show any evidence of fasciation, the development in either case being essentially the same as that of any ordinary floral or vegetative shoot. The only kind of organ of which we have any knowledge, the like of which could have united to form an ear, is the lateral branch of the tassel, and this involves a mathematical difficulty. The rows of grains on an ear are paired because the spikelets are borne in pairs. If a lateral spike of the tassel should contribute to the formation of an ear anything in terms of paired spikelets, it would be responsible for *four* rows, and this would make impossible an ear of ten, fourteen, or eighteen rows; but the fact remains that such ears are common. Harshberger's idea that each pair of rows of grains corresponds to a spike of *Euchlaena* or *Tripsacum* is of no avail in getting around this difficulty; they bear two rows of functional spikelets, but not at all because of the presence of paired spikelets, for one spikelet of each pair is rudimentary. It may be noted, too, that although Worsdell has the ear formed by the union of spikes bearing *two* rows of spikelets, he has it "disrupt" into a central spike bearing eight rows and a number of lateral spikes each bearing *four* rows (**28**, *pl. 39, f. 13*). Incidentally it may be said that the "disrupted" ear figured is not *abnormal* at all but a normal tassel of a sucker.

Collins (**9**, p. 526) advances another theory which probably offers the best explanation of the origin of both of the organs in question. He suggests that the male inflorescence might have been developed from a loose panicle by the shortening of some of the branches until pairs of spikelets were left on a central spike and a few lateral branches; the ear could easily have been developed from this by the loss of the side branches. He abandons this theory for want of sufficient evidence in the form of intermediate steps, but Gernert's Branch Corn (FIGS. 14–19) supplies the needed evidence and strengthens a very consistent theory.

Hybrid origin of maize.—A new variety of corn known as *Zea canina* was reported from Mexico about 1890, and Bailey (1) and Harshberger (17) concluded that it was the long-sought wild ancestor of the species, the latter making it the basis of his monograph on corn. But correspondence with Mexicans who knew the plant showed that *Zea canina* could be produced at will by hybridizing teosinte and ordinary maize. Accordingly, previous conclusions had to be revised, and along with Harshberger's revision (18) came the suggestion of three possible explanations of the botanical nature of maize: (1) that maize is a distinct species; (2) that maize originated as a hybrid between teosinte and some unknown grass; and (3) that maize is the result of a cross between teosinte and some variety of teosinte which had been changed by cultivation. He favors the last-named possibility, and in his latest expression on the subject (21, pp. 398–399) this is the only theory given.

His conclusions were reached as a result of hybridization experiments with maize and teosinte, in which a graded series of intermediates between the ear of the one and the female spike of the other were produced. A series of this kind always suggests evolution, but this one does not possess the advantage of having maize at one end and its two hypothetical ancestors at the other. Moreover, the status of the hybridization problem at the time at which this theory was proposed (1896) and the evolutionary influences attributed to cultivation, especially to irrigation, do not show up so well alongside the genetics of this later day.

Collins's theory (9) is similar to the second possibility suggested by Harshberger; that is, he thinks that maize originated in a cross between teosinte and some unknown grass similar to pod corn and belonging to the Andropogoneae. With respect to a large number of characteristics, ordinary maize is shown to be intermediate between the primitive pod corn and the highly specialized teosinte; and this is considered evidence that *Zea* is a hybrid between the two extremes.

Although this theory is the most elaborate and the most widely accepted of all the attempts that have been made to explain the origin of maize, yet it falls short of its aim in some respects. Granting the accuracy of the observations upon which

it is based, we may still question the value of the facts as constructive evidence leading to the conclusion. Is it safe to assume on this basis alone that an intermediate of this kind is necessarily a hybrid between the two extremes? And is a hybrid usually intermediate in character between its parents? But many of the supposed facts upon which this theory is based will not stand the light of a close examination; and the actual conditions are capable of a more simple and more direct explanation in another way.

The theory depends upon some hypothetical pure variety of pod corn, which can be approached in reality only by inbreeding some one of the many available genetic complexes commonly known as pod corn. But inbreeding for purity implies intelligent selection among the pure lines reached or approached; and this places a burden of responsibility upon him who makes such selection the basis of a theory of this kind. Collins has in mind, however, some strain of pod corn the like of which he considers one of the ancestors of maize; and, in describing its simple, primitive nature, he makes some statements which are not in accord with the morphological facts that I have already set forth. The extreme type of pod corn is described (9, p. 527) as having no ear, the absence of branches being a primitive characteristic. Disregarding the difficulty occasioned by the fact that these earless plants are incapable of self-propagation, we may cite the fact that they have buds in the axils of their leaves, indicating the suppression of ears. If a plant that never had any ears is primitive, one that has vestiges of ears that it has lost must be highly specialized. He says (p. 528): "In the branched forms of pod corn staminate flowers have never been observed on any of the branches." Contrary to this is the fact that sucker branches of pod corn often bear mixed or staminate inflorescences, these having often been mistaken, no doubt, for earless plants, especially when more than one plant is grown in a hill; and in several cases ears of pod corn have been found bearing well-developed stamens. Applying the specialization test to the ears, he says (p. 528): "In pod corn branches have never been observed in the axils of prophylla;" but I have often seen such branches, especially when the main ear had been injured and buds are to be found in the axils of the husks of all kinds of corn. From the foregoing cita-

tions it may be seen that Collins does not necessarily hold to any one variety of pod corn for his evidence, switching from earless to branched types as he finds structures to fit his hypothesis; and, even with this latitude of choice, he fails to find sufficient evidence that pod corn is wholly primitive. It is readily granted by anyone that the tunicate character and the tendency toward hermaphroditism are primitive characters, but otherwise the plant is modern, as the fasciated silk, the husks of the ear, and the many degenerate organs go to show. The earless plants are the most highly specialized of all, as indicated by the vestigial ear-buds in the axils of their leaves.

Similar inconsistencies occur in the description of teosinte, which is held to be highly specialized; the mention of a single example will be sufficient. In support of a detailed argument that the extreme differentiation between the male and female inflorescences of teosinte points toward specialization higher than that in maize, he says (p. 524) that female flowers have never been observed in the male inflorescence of *Euchlaena*. I have already described mixed inflorescences of this plant; but the importance of this point is diminished by the fact that in this entire group of plants we are dealing with flowers which are structurally bisexual.

Readily granting that monoecism is a less fixed characteristic and that the separation of male and female flowers is not so sharp in maize as in teosinte, yet I do not believe that pod corn has been shown to be sufficiently different from ordinary corn to merit the prominent position that it holds in this theory.

In a recent report on this theory (11) the intolerance of self-pollination in maize is given as another evidence of its hybrid nature, it being almost if not quite unique among the grasses in this respect. But possibly another explanation for this may be found in its having a very small number of monoecious inflorescences and, because of protandry or protogyny, a limited chance for self-pollination under normal conditions, in which respect it is also unique among the grasses. All the other members of the Maydeae, teosinte, for example, produce a large number of inflorescences and have a flowering period much longer than that of maize, the chances for self-pollination being correspondingly

better. *Tripsacum* can be excluded from this consideration because it depends mostly upon vegetative propagation for increase in number of individuals. In those grasses which have perfect flowers self-pollination is the rule. Tolerance of self-pollination may thus be interpreted as a matter of adjustment to the conditions which have prevailed during the development of the plant in question.

Traumatic evolution.—Maize was one of the principal plants considered by Blaringhem (**3**, **4**, **5**) in arriving at his theory of mutation by traumatic influences, and his conclusion as to its evolution may best be stated in his own words (**6**, p. 228): "L'étude des variations observées à la suite de mutilations permet de reconstituer l'évolution du genre *Zea*, et d'établir que l'ancêtre sauvage du Maïs cultivé est l'espèce *Euchlaena mexicana*. Le genre *Zea* est une forme monstreuse du genre *Euchlaena* née et propagée par les soins de l'homme." The chief interest in his work in this connection lies not so much in his contribution to our knowledge of the evolution of the plant as in the peculiar methods employed and the peculiar interpretation of results.

By mutilating plants in various ways he causes them to send up sprouts whose terminal inflorescences bear both male and female flowers. Seeds from these sprouts provide the starting points for numerous new varieties characterized by such peculiarities as suckers with mixed inflorescences, ears with perfect flowers, branched ears, tubular leaf sheaths, etc. Many of these breed true and are given the rank of elementary species, a number of new varietal names being contributed to the already overburdened list associated with the variations of this monotypic genus. Throughout the discussion, the sucker bearing a female or mixed inflorescence is considered an abnormality; but if this is the correct interpretation for the suckers of the whole genus, it constitutes a case where the exception is quite as common as the rule. In his description of the spikelets of the normal plant (**6**, p. 21) he states that neither the male nor the female flower contains organs of the opposite sex; and this fallacy becomes the basis for his assumption (**5**, p. 1253) that the acquisition of perfect flowers by some of his new varieties constitutes a *progressive* step. No change that he has produced in the plant involves any charac-

teristic that is actually new, and, as Gernert suggests (14, p. 6), most of the results may be explained on a basis in no way connected with the original mutilation. As the theory stands, we can justly ask that the experiments be repeated successfully with more than one variety of maize, and the results interpreted on the basis of a more sound understanding of the morphology of the plant throughout its normal range of variation, before we consider this a substantiated explanation of the past history and present tendencies of the plant.

Montgomery's theory.—Along with his explanation of the ear of corn as the homologue of the central spike of the tassel (24), Montgomery proposes a theory of evolution, which, while not worked out in full detail, is probably the most consistent solution of the problem yet offered. He considers maize a distinct genus coördinate with teosinte, both having developed from a common teosinte-like ancestor.

A THEORY BASED UPON MORFHOLOGY

Exact knowledge of the past conditions being out of the question, the ancestry of the maize plant and the steps taken in its evolution can only be built up in theory from a study of the modern plant and its near relatives; and some attempts previously made in this direction have already been discussed. Any theory that is to receive serious consideration must be based upon, and consistent with, recognized facts; and, of two or more explanations of the same thing, the simplest and most direct is to be preferred. Several kinds of evidence are available for use in the study of maize; but morphology, the basic constructive factor of most of our theories of evolution, has never been utilized to the full extent. To be sure, the gross structure of this group of plants has several times been considered, but a morphological study that does not go to the bottom of the question is likely to mislead the investigator. The study of abnormal structures is always instructive, but it is more significant to find in the normal plant a morphological basis for its abnormalities. Other considerations, such as may be occasioned by experiments in hybridization and selection for a few generations, constitute instructive checks on other methods; but they must not be over-emphasized as constructive

material, and they are never any better than the morphology upon which they are based.

Ancestry of maize.—It is neither necessary nor desirable, I believe, to look for the ancestor of maize and its near relatives in any plant now living; its evolution along different lines to the present forms would imply its own probable disappearance. There are found in different members of the Andropogoneae, however, all the characteristics necessary for a theoretical progenitor of maize and its American relatives. In the evolution of these plants from their common ancestor, many steps were probably taken, no suggestion of which has passed down to modern times. It is almost certain that the Asiatic species of the Maydeae arose from this same stock, and many lines of descent may have led to other forms now long extinct. Geology and archeology are of little value to us in solving these problems, since the oldest remains of these plants found in the rocks or in human habitations are practically modern.

Theoretically the ancestor of these plants was an herbaceous perennial, whose tall, jointed, leafy stems sprang from a rhizome. A branch was borne at practically every node of the aërial stem, each being somewhat shorter than the main stem and having about as many nodes as the latter above the point of branching. Branches upon branches occurred to the third and fourth or higher orders. The main stem and each branch was terminated by a loose, ovoid or pointed, monopodially branched panicle. In this panicle the spikelets were probably borne in pairs, one sessile and one pedicelled, in many irregular peduncled clusters on the main axis and its branches. Each spikelet had two perfect flowers; the pistil had two feathery stigmas. From this plant the three genera here considered, and probably the other genera of the Maydeae and some of the Andropogoneae as well, have been evolved by the *suppression of parts*, whose rudiments are, in most instances, still to be found in the modern plants.

The cause of this suppression and the mechanism of its accomplishment are unsolved problems, but the phenomenon is not peculiar to this group of plants alone. It is known that monoecism among the angiosperms has been reached independently in many groups as a result of the suppression of one set of organs in each

flower; and the suppression of whole inflorescences and of vegetative parts is also common. Whether this suppression is due to environment, or to inherent tendencies, or to a selection by the environment among the results of inherent tendencies, is unknown; but the comparative structure of *Zea*, *Euchlaena*, and *Tripsacum* indicates that, in their development from a common ancestor, certain tendencies have found expression in different ways in the different genera; and this expression has often come in the nature of a response to external conditions. In other words, we assume that these three genera are closely related, not because the characteristics which they have were present in a common ancestor, but because they have been evolved from an ancestor which had tendencies to suppress pistils in some flowers and stamens in others, whole flowers in some cases, and in some cases vegetative organs. Unless this assumption is made, we cannot base any close relationship between *Euchlaena* and *Tripsacum* upon monoecism, for the separation of the sexes in these two genera has been accomplished in different ways.

The first division of the progeny of this ancestral form set off a group in which the upper spikelet of each pair had lost its pistils, this giving rise to a number of genera of the Andropogoneae. On the other hand, in some of the plants whose inflorescences had retained their perfect flowers, the peduncles bearing groups of spikelets grew shorter (FIGS. 15–19) until the spikelets were arranged as in the tassels of maize or teosinte (FIGS. 3, 4, 5, 21). Pairs or larger groups of spikelets could have been left in this way. The plants in which the central spike of the inflorescence survived this process became the ancestors of *Zea;* while those in which this spike was lost gave rise to *Euchlaena* and *Tripsacum*. In the separation of these two genera, two lines of evolution were followed, depending upon the manner in which monoecism came about.

Origin of Euchlaena.—In the line tending toward *Euchlaena*, the uppermost inflorescences—those terminating the main branches—lost their female elements and assumed the form of the present teosinte tassel (FIG. 20), while the lower inflorescences lost their male elements; between these two extremes were formed some mixed spikes, the upper portions being staminate and the lower

pistillate. In the pistillate spikes, or portions of spikes, the pedicelled spikelet and the lower flower of the sessile one became aborted (FIGS. 27, 28). Each branch bearing a female inflorescence shortened enough that the inflorescence was covered by the sheath of the leaf just below it; at the same time, all but one (or rarely more) of the spikes of this inflorescence disappeared, and the two stigmas of each pistil, lying side by side and elongating to keep their tips exposed beyond the enveloping leaf sheath, united, except at their exposed tips, to form the silk. The brittle rachis came with the hardening of the outer glume of the spikelet and the walls of the alveolus in which the spikelet was imbedded. The leaf whose sheath enclosed the female spike has since then almost lost its lamina (FIG. 25). By a continued shortening of the internodes, the sheaths of lower and larger leaves were later caused to envelop clusters of these simple female spikes and their husks (FIG. 26). There is nothing to indicate when *Euchlaena* became an annual, but this habit is probably correlated with a reduced supply of moisture.

Origin of Tripsacum.—In those individuals tending toward *Tripsacum*, monoecism came about as a result of the loss of female elements from the upper part and male elements from the lower part of each spike of the inflorescence (FIG. 32). The point of division between the male and female portions of a spike was higher in the inflorescences of the branches than in that of the main stem. In the male portion, the pedicellate spikelet became almost sessile; the female portion became essentially as in teosinte. There was no appreciable shortening of any internodes, and the inflorescence was not covered by a leaf sheath; consequently there was no reduction in the number of its branches, and the two stigmas have persisted (FIG. 31). This plant usually grows in rich, wet soil, and it has remained perennial; its ability to produce viable seeds is restricted.

Origin of Zea.—In the evolution of *Zea* from its progenitor, the inflorescence terminating the main stem lost its female elements and approached its present form (FIG. 2). Those terminating some of the primary branches near the middle of the main stem lost their male elements, and these branches began to shorten their internodes. As this shortening continued, the secondary

branches were reduced to buds; and, as the leaf sheaths began to enclose the terminal inflorescence of the branch, this inflorescence lost its lateral branches, only the central spike remaining. Up to this time the mature fruits were covered by the palets and glumes, but, as a response to the covering of husks, these bracts became shorter, leaving the mature fruits naked except for the husks of the ear. The leaves whose sheaths formed the husks, tended to lose their laminae and ligules (FIG. 7); these remain, however, in some varieties (FIG. 6). The two stigmas united, as in teosinte, to form the silk. At some time in the development of the ear, the lower flower of each female spikelet lost its function, but when and why this occurred is not clear at present. Probably all the primary branches of the stem, except those low enough to take root, went through this process, and most of them became still further reduced; at present, one to five or six usually remain as ears, and the rest have been reduced to buds in the axils of the leaves of the main stem. Those primary branches low enough to take root (FIG. 1) did so and have met with the varied fate characteristic of the suckers of the plant. Some are like the main stalk and others like ears, depending probably upon their relative independence; but the great majority share the characteristics of both (FIGS. 11–13).

Meaning of variations in maize.—In the light of this theoretical history of the species we are able to interpret many of the ordinary variations of maize. The podded ear is a reversion to the condition of the ear unprotected by husks, and very probably not a primitive form that has come down to us unchanged. Grains in the tassel mark a resumed function of the pistils in the male flowers, and they are usually characterized by the fasciated silk, showing that their flowers have not reverted in all characteristics. Gernert's Branch Corn (15) is a reversion to the primitive paniculate inflorescence by a plant which is modern in other respects. Emerson's dwarf variety (13) and one of Blaringhem's new varieties (5), both of which have perfect flowers in the ear, are, in so far as the perfect flowers are concerned, analogous to the varieties with perfect flowers in the tassel. Two-flowered female spikelets, such as those regularly found in Country Gentleman sweet corn (25, p. 135) and a few other varieties, are

reversions to the primitive two-flowered condition. We should not expect any one plant to show reversion in all respects; characteristics probably behave as units in reversion as much as in heredity.

Some freaks, such as ears divided at the tip (**17**, p. 81; **14**, p. 37) and fasciated kernels (**27**), are probably best interpreted as anomalies of ontogeny, giving no more clue to the past than is afforded by Siamese twins or lilies with two-parted flowers. Indeed, an ancestral form that would be consistent with all the teratological ears that have been used as evidence would be an impossibility. It is a fact worth mentioning, also, that many of the teratological conditions that do not fit into the foregoing theory as reversions are not inherited, while those in accord with this theory often form the starting points of new varieties tending to breed true.

It is not deemed advisable here to attempt to trace the probable origin of all the more or less fixed varieties of corn that have come into existence after the generic characteristics were reached; but no constant characteristic is known in any variety, which is inconsistent with the general theory here outlined. The development of the annual habit was similar to that of teosinte, and no further explanation is offered. The restricted period of flowering has a morphological cause in the reduced number of inflorescences.

CONCLUSION

It is granted that the foregoing theory involves a measure of speculation, but that is to be expected of any theory; it is as conservative as any that have been advanced to explain the origin of maize, and much more so than some of them. It is believed to be a logical deduction from the best and most recent evidences available, and in it are embodied parts of some of its predecessors. No point in it is known to be out of harmony with a rational interpretation of any established fact of structure, history, or genetic behavior concerning the plants with which it deals.

How much of this evolution of maize was due to natural agencies, and how much to the influence of primitive agriculture, we have no means of knowing; but, from the botanical point of view, the changes wrought by four hundred years of civilization

FIG. 36. A corn plant very highly specialized by scientific breeding. The suckers have all been lost, and the entire energy of the plant is directed toward the production of a single large ear.

are insignificant as compared with those preceding the advent of the white man. The varieties of corn which Columbus first saw in the West Indies in the fifteenth century were probably in no essential way different from those now grown on many Indian reservations (FIG. 1); and the highest attainment of corn breeding, as represented by the dent varieties of the Mississippi valley today (FIGS. 7, 36), is merely one of a combination of these varieties, with a few more organs dropped, a little more concentrated fructification, and a little greater vegetative vigor.

SUMMARY

Vestigial organs being considered, *Zea*, *Euchlaena*, and *Tripsacum* are identical in structural plan. The present aspect of each is due to the suppression of some parts which were present in a primitive ancestor having perfect flowers borne in one type of inflorescence.

The ear of maize is the homologue of the central spike of the tassel. There is no morphological evidence to support the view that either of these organs originated in the fusion of more simple parts; and there is in no one of the genera here considered any organ the like of which could have united to form either the ear or the central spike of the tassel.

The prevailing theory that maize is a species of hybrid origin has little to suggest it when maize and its near relatives are thoroughly understood, and it is not in harmony with the most significant facts of morphology. It seems much more probable that *Zea*, *Euchlaena*, and *Tripsacum* have descended independently from a common ancestral form now extinct.

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The relationship between the number of sporophylls and the numbers of stamens and pistils—a criticism

HELENE M. BOAS

In a paper entitled, "The interrelationship of the number of stamens and pistils in the flowers of *Ficaria*," Harris* has attempted, by statistical methods, to throw some light on the biological factors which determine the sex of an organism. The relative numbers of pistils and stamens present are assumed to indicate which sex is more influenced as the total number of sporophylls increases. Without a knowledge of the number of functional spores that are produced the ratio of the two kinds of sporophylls can hardly be considered as a fundamental measure of the sex of a flower. Nevertheless the quantitative relations between stamens and pistils, if handled so as to be of biological and not purely statistical significance, may suggest more precisely the factors that influence the development of the two sexes.

Harris correlates the deviations of the total number of sporophylls and those of the pistils and stamens from their "probable values." He means by this the average frequency of pistils and stamens to be expected according to the total number of sporophylls. He does this rather than correlate directly with the numbers of pistils and stamens in order to eliminate, as he believes, the spurious correlation which would exist in the latter case. He finds the correlation between the number of sporophylls and the deviation of the pistils from their "probable number" to be of equal magnitude to that of the stamens, but positive, while that of the stamens is negative. From this he concludes that as the number of sporophylls increases, the pistils increase relatively more rapidly than the stamens.

It can be shown that this result necessarily follows from the fact that there are more stamens than pistils while their varia-

* Biol. Bull. 34: 7–17. 1918.

bilities are almost equal, and consequently has only mathematical and not biological significance.

According to Harris's formula, if $(n + s)$ represents the mean number of sporophylls with their deviations and, let us say, p the percentage of pistils and z_p their deviations from their "probable number" the pistils would be represented by the formula $(n + s)p + z_p$, and the stamens by the formula $(n + s)(1 - p) - z_s$, where z_s is the deviation of the stamens from their "probable number" and $z_s = z_p$. The sum of the pistils and stamens must, of course, equal $(n + s)$, the total number of sporophylls. He then correlates the variables s and z, assuming that z is not contained in s.

We may analyze Harris's formula for pistils to determine which values are known and which are unknown. If n represents the average total number of sporophylls, n_p that of pistils, n_s that of stamens then $n = n_p + n_s$. $n_p + x$ are the pistils with their deviations, $n_s + y$ the stamens with their deviations. The deviation of the total number of sporophylls from their mean, s, equals $x + y$; so that Harris's value for sporophylls $(n + s) = n_p + n_s + x + y$. Since p represents the percentage of pistils, it is equal to $n_p/(n_p + n_s)$, and Harris's value for pistils, given above, becomes

$$(n + x + y)\frac{n_p}{n_p + n_s} + z_p$$

z_p is the only unknown value. We may find its value from the following equation:

$$(n + x + y)\frac{n_p}{n_p + n_s} + z_p = n_p + x,$$

the number of pistils plus their deviation. Solving this

$$z_p = \frac{n_s x - n_p y}{n_p + n_s},$$

$$s = x + y.$$

Therefore, correlating s, the total number of sporophylls, with z_p, the deviation of the pistils from their "probable value,"

$$z_p s = \frac{n_s x - n_p y}{n_p + n_s}(x + y)$$

and averaging

$$[z_p s] = \frac{n_s\sigma_x^2 - n_p\sigma_y^2 + (n_s - n_p)r\sigma_x\sigma_y}{n_p + n_s}.$$

According to Harris's result $[z_p s]$ is always positive. The formula shows that this must be the case when

$$n_s\sigma_x^2 - n_p\sigma_y^2 + (n_s - n_p)r\sigma_x\sigma_y > 0$$

or when

$$n_s(\sigma_x^2 + r\sigma_x\sigma_y) > n_p(\sigma_y^2 + r\sigma_x\sigma_y).$$

If σ_x and σ_y are equal this can happen only when $n_s > n_p$, or in other words when the stamens are more numerous than the pistils.

From the original data from which Harris has drawn the material for this study (see Harris for references) it is evident that the standard deviations for pistils and stamens are nearly equal and that the stamens are more numerous than the pistils. For the average values for Europe given by Pearson the mean number of pistils is 19.432 with a standard deviation of $\pm$ 4.8508; the mean number for stamens 26.498 with a standard deviation of $\pm$ 4.2562. The coefficient of correlation is + 0.5584. Substituting these values we find the results obtained by Harris necessarily follow from the existing numerical relations.

From this consideration it seems evident that the results obtained by Harris do not add anything to the observations on the numbers of pistils and stamens and their variabilities. Just so the higher coefficients of variation given by Harris in Table I of his paper result from the fact that the same value (standard deviation) is divided in the case of the pistils by a lower value (mean for pistils) than in the case of the stamens (mean for stamens).

It might be said that the total number of sporophylls and the per cent of stamens and pistils vary independently, in which case the expression $(n + s)(p + v)$ would represent the number of pistils. Disregarding the value sv, since it is small in comparison to the other values, the expression becomes $p(n + s) + nv$ and the same relations will hold as in the case discussed above.

NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE

1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

This Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of one cent for each card. Selections of cards are not permitted; each subscriber must take all cards published during the term of his subscription. Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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New species are described in *Uromyces* (2), *Puccinia* (8), *Aecidium* (10), and *Uredo* (3).

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New species are described in *Ravenelia* (1), *Uromyces* (3), *Puccinia* (13), *Aecidium* (3), and *Uredo* (2).

Arthur, J. C. Uredinales of the Andes, based on collections by Dr. and Mrs. Rose. Bot. Gaz. **65**: 460–474. 15 My 1918.

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Vaccinium Margarettae sp. nov. is described.

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Twenty-four new species are described.

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Fairman, C. E. Notes on new species of fungi from various localities—II. Mycologia **10**: 164–167. My 1918.
Includes new species in *Phoma* (1), *Phomopsis* (1), *Sphaeropsis* (2), *Camarosporium* (1), *Rhabdospora* (1), *Microdiplodia* (1), *Hendersonia* (1), *Dictyochora* (1), *Platystomum* (1).

Fernald, M. L. *Rosa blanda* and its allies of northern Maine and adjacent Canada. Rhodora **20**: 90–96. 1 My 1918.
Rosa johannensis and *R. Williamsii*, spp. nov., are described.

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Includes new species in *Cercospora* (1), *Coryneum* (1), *Cryptospora* (1), *Cryptosporium* (1), *Dendrodochium* (1), *Diplodia* (2), *Eutypella* (1), *Gloeosporium* (1), *Leptosphaeria* (1), *Massarinula* (1), *Microdiplodia* (1), *Phoma* (1), *Ramularia* (1), *Septoria* (3), *Sphaeropsis* (3).

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Six new species are described.

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New species are described in *Puccinia* (3), *Septoria* (1), *Cercospora* (1), and *Helmintosporium* (1).

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One new species and many new varieties and new hybrids are described.

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